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Learning Expands the Preplanning Horizon in Finger Sequence Tasks

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Abstract

Many everyday skills involve the production of complex sequences of movements. However, the dynamics of the interplay between action selection and execution processes in sequential movements is poorly understood. Here, we set out to investigate the extent to which information regarding upcoming actions is utilized by the motor system to preplan into the future and furthermore, how this ability is influenced by learning. We designed a finger sequence task where participants were shown only a fixed number of upcoming cues regarding future presses in every trial (viewing window, W). W varied between 1 (next digit revealed with pressing the current digit – classical discrete sequence production task, DSP) to full view of the sequence. Each participant underwent 5 sessions of training. Our results clearly indicate that participants selected and prepared multiple actions into the future. On day 1, when the effect of practice is minimal, participants performed significantly slower for window sizes 1 and 2, compared to a fully visible sequence. This suggests that information regarding up to 2 digits ahead was used to preplan upcoming actions. Furthermore, our results show that for larger window sizes, performance benefits from practice to a higher extent compared to smaller window sizes. This suggests that in addition to more efficient stimulus-to-response mapping, a large part of sequence-nonspecific learning is explained by using in-advance information more effectively. This claim is supported by the fact that the span of preplanning, i.e. the preplanning horizon size increased from 2 digits ahead in the early phase of learning to 4 digits ahead in the late learning phase. Finally, we show that the observations of this study can be successfully modelled using a relatively simple race model of action selection, with the ability to preplan multiple actions into the future in parallel with action execution.

Keywords

Finger sequence task, discrete sequence production, skill learning, hand function, motor planning, preplanning horizon

Co-Authorship Statement

I, Neda Kordjazi, am submitting this research project as partial fulfillment of the Master of Science Degree in the discipline of Neuroscience. As such, I have had the primary role in all aspects of this document including, but not limited to, laboratory setup, experimental design, data collection and analysis, as well as producing the initial draft of the thesis. I collected and analyzed all of the data, and performed all of the statistical analysis. Dr. Jörn Diedrichsen acted as my supervisor for this project. He provided critical advice throughout all stages, and also acted as an editor to the subsequent drafts of this thesis.

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1 Introduction

Humans use a wide variety of motor skills on a daily basis; from walking and riding a bike to fine dexterous skills like typing or playing the piano. When learning a new skill, many hours of practice are needed to achieve proficiency and fluidity in performance (Diedrichsen & Kornysheva 2015). An abundance of research has been dedicated to examining effects of practice on behavior (Lashley 1951; Verwey 2001; Krakauer et al. 2000; Verstynen & Sabes 2011; Wulf et al. 2001; Müller & Sternad 2004), some of which include increase in accuracy and speed of task performance, reduced variability in behavior, decrease in cognitive workload, automaticity and habit formation. However, there is still very little clarity or agreement regarding the underlying mechanism leading to these behavioral changes (Wolpert & Flanagan 2016; Haith & Krakauer 2018; Magnuson et al. 2010; Haith et al. 2016; Sheahan et al. 2016; Marblestone et al. 2016; Kriegeskorte & Diedrichsen 2018).

Despite their distinct characteristics, most motor skills share one feature: they are comprised of a series of separate motor elements, concatenated in order, to from longer and more complex movement or essentially motor sequences (Lashley 1951). Therefore, the process of learning to execute the single elements of a new movement in rapid succession or motor sequence learning (MSL) has been utilized as a model to study skill acquisition in lab settings (Lashley 1951; Wiestler & Diedrichsen 2013; Verwey 2001; Doyon et al. 2018). Finger sequence tasks for instance, are often utilized to study skilled hand function. In a typical finger sequence task certain features in the stimuli (S) e.g., numbers, colors, locations, etc. correspond to certain responses (R) made by individual finger presses (Diedrichsen & Kornysheva 2015). Critically, although the instructions of such a task are logically simple enough for naïve subjects to follow, the task is very flexible and provides solid grounds for a wide variety of paradigms with buildable complexity.

1.1 Learning in finger sequence tasks

Traditionally, finger sequence tasks fall into two main designs; a) serial reaction time (SRT) task, and b) discrete sequence production (DSP) task.

SRT in its most basic appearance (Nissen & Bullemer 1987) is a continuous four-choice reaction time (RT) task in which participants respond to the location of the stimulus. Normally a fixed response-to-stimulus interval separates successive cue presentations. Unbeknownst to the participants, individual cues either follow a certain rule or are presented as a fixed-length sequence that is repeated continuously. Various modified versions of the SRT task have been designed since to test specific hypotheses and mechanisms of learning.

Regardless of the specifics of the SRT task, it is typically shown that performance shows a much larger improvement for familiar compared to unfamiliar sequences. To quantify the magnitude of sequence-specific learning, it is common to include a random sequence block in the post-test (Keele et al. 2003a; Haider et al. 2018), and measure the difference between performance in the random compared to familiar sequences. Participants perform substantially better in familiar sequences compared to random, substantiated in better performance measure, like seed and accuracy. This points to formation of a level of sequence specific knowledge. However, when asked to verbally recall or recognize the stimuli of the familiar sequences, subjects are often unable to (fully) express their knowledge. Therefore, the sequence-specific learning in SRT is characterized as *implicit* (Cleeremans et al. 1998). In this sense implicit learning is defined as the development of associations between stimuli and/or responses, referred to learning in associative mode (Verwey & Abrahamse 2012; Perruchet & Pacton 2006), rather than knowingly learning a particular motor sequence.

It is thought that in these association firstly start shaping between stimuli and their corresponding responses (stimulus-response mapping) (Schwarb & Schumacher 2010). This type of learning presumably promotes better performance in both familiar and random sequences and furthermore, is completely explicit, meaning subject are perfectly able to verbally declare which stimulus maps to which response. However, as practice progresses and with repeated exposure to familiar sequences, a second and slower component of associative learning develops: the stimulus-stimulus and response-response associations (Verwey et al. 2014). This component of associative learning is the key mechanism that implicit learning in SRT is attributed to.

The DSP task on the other hand, first introduced by Verwey (Verwey 2001), has been utilized mainly to study role of explicit or declarative knowledge of the familiar sequences in

motor sequence learning and performance, also referred to as *explicit learning* (Verwey & Wright 2014; Verwey 2001). To this end, as one main methodological feature, the DSP task starts off with a practice phase. The purpose of the practice phase is to form explicit knowledge of the sequences either as a whole (Verwey et al. 2014), or in small segments that will later be concatenated (Verwey 2001). In the DSP design participants are instructed to execute sequences as fast as possible, either from memory (Wiestler et al. 2014) or supported by sequential cues (Verwey et al. 2014; Rhodes et al. 2004; Abrahamse et al. 2013). Here, quite similarly to the SRT, the sequence specific effects of learning are measured in comparison to unfamiliar sequences in the post-test phase. However, in contrast to SRT, the sequence specific part of learning in DSP is mainly attributed to the formation of *motor chunks*. A motor chunk is defined as a group of successive movements that are selected, initiated and executed as if they constitute a single response (Diedrichsen & Kornysheva 2015). Motor chunks are thought to form as the result of repetitive exposure to the same succession of stimuli and/or responses during the practice phase (Verwey & Wright 2014) Thus, chunking mode results in relatively increased time intervals on the chunk boundaries, followed by a series of fast within-chunk key-presses. Therefore, motor chunks are classically detected by finding the reoccurring temporal groupings between responses to certain stimuli.

1.2 Current opinion and historical review

Regardless of the task setup, one unquestionable aspect of sequence learning is the ability to select and execute appropriate actions, in response to their corresponding stimuli (Diedrichsen & Kornysheva 2015). With this in mind, performing in a continuous and steady manner would require the motor system to harmonize the interplay between ongoing selection and execution processes. An obvious outcome of this orchestration is the fluidity seen in behavior (Wolpert & Flanagan 2016).

The fact that benefits of practice on performance are substantially more pronounced in familiar sequences compared to the unfamiliar ones both in DSP and SRT, suggests that participants acquire a level of knowledge about the structure of the familiar sequences. In this

sense, unfamiliar sequences are generally used as no further than a frame of comparison for trained sequences.

Interestingly, most studies incorporating either SRT or the DSP, show nonexistent or very small and non-significant effect of practice in the unfamiliar sequences over the course of training (Nissen & Bullemer 1987; Keele et al. 2003b; Haider et al. 2018; Verwey et al. 2014; Rhodes et al. 2004; Abrahamse et al. 2013; Moisello et al. 2009; Verwey & Abrahamse 2012; Ghilardi et al. 2009; Deroost & Soetens 2006). Responding to individual stimuli in entirely unfamiliar sequences is said to be carried out in *reaction mode* (Verwey & Abrahamse 2012), where subjects translate every stimulus into its appropriate response one-by-one (Hikosaka et al. 1999). As per the *Dual Processor Model*, proposed by Verwey et. al. (Verwey 2001), such execution involves two successive processing steps for every individual press: response selection and response execution. A response is selected and prepared by a *cognitive processor*, which receives the stimulus and translates it into an appropriate response on the basis of task instructions. The prepared responses are then loaded onto a short-term (motor) buffer to await execution. Second, the prepared action is retrieved from the buffer by the *motor processor* and subsequently executed. This process is also known as stimulus-to-response or S-R mapping. Improvement in S-R mapping has been shown in reaching tasks (Haith et al. 2016). However, the fact that no substantial effect of learning has been demonstrated in unfamiliar sequences suggests that in the context of the existing finger sequence task designs, the motor system shows only very limited improvement in individual S-R mappings. This in turn could potentially indicate that in this case, S-R mapping is by and large governed by somewhat fixed parameters in the motor system that typically exhibit no or slow effects of practice, e.g. sensory transmission delays, as well as sensorimotor delays (Franklin & Wolpert 2011), as well as other parameters like habit and procrastination (Wong et al. 2017).

Therefore, a critical question to ask is whether motor learning can employ additional mechanisms, beyond individual S-R mappings, to improve performance in unfamiliar sequences. Both SRT and DSP tasks, in their most classical form, allow the participants to see the upcoming cue in the sequence, only after responding to the previous cue. With the distinction that in the SRT task the previous cue disappears after being responded, so that the subject can only see one stimulus on the screen at any given time (Moisello et al. 2009). In

the DSP design however, either the previous cues in the sequence stay in sight (Abrahamse et al. 2013), or subjects undergo a practice phase to allow the formation of explicit sequence knowledge.

The absence of practice effects in unfamiliar sequences has also been shown in a version of the DSP design (Verwey & Dronkers 2018), where the next cue in the sequences is revealed either simultaneously (no-delay group), or after fixed delays (delayed group) from the previous response.

This study reveals that at the end of the training period, participants in both the delayed and the no-delay groups showed faster execution in familiar compared to unfamiliar sequences, however this sequence-specific learning is execution rate-specific. Meaning the no-delay group did not show the same learning effects in a delayed post-test. A similar outcome holds for the delayed group in a no-delay post-test. Critically, the same study shows that the no-delay group shows a significantly faster response time for unfamiliar sequences compared to the delayed group at the end of training. This suggests that the no-delay group gained some general, sequence-unspecific skill to produce discrete keying sequences. Furthermore, a recent experiment by Wiestler et. al. with several trained and untrained sequences does show a noticeable general effect of learning in untrained sequences (Wiestler et al. 2014) . Importantly, in this study all the stimuli in the sequence are revealed to the subjects at once at the beginning of every trial, and additionally the stimuli stay on the screen throughout the trial. Taken together, these studies suggest that the way in which the sequence cues are revealed to the subjects is of critical importance, not only to the sequence-specific effects of learning, but also to the general practice effects in unfamiliar sequences.

The current literature attributes the improvement in performing unfamiliar sequences mainly to improved S-R mappings. The prominent emphasis on serial S-R mappings can be traced back to the associative chaining theory, an early behaviourist theory which claimed that action sequences were represented as series of unidirectional S−R links, chained together in one smooth performance. In other words, each element in the sequence, provides the excitation of the next. The appeal of this type of account is its simplicity; it requires no more than a representation of the stimuli and the Hebbian links from stimuli to responses. Hence,

retrieval of a sequence is achieved by tracing a path through the links. It should be noted that in this account, parallel preplanning of multiple actions into the future is not plausible.

In a well−known article published in 1951, "The Problem of Serial Order in Behavior", Karl Lashley (Lashley 1952) pointed out that sequential organization of actions is critical to much of animal and human behavior, from locomotion, through reaching and grasping to language and the control of logical reasoning. However, this organization could not be attributed to one by one activation of serially ordered responses, but rather depends upon internal organizing principles by which the execution of the actions is controlled.

He postulated that the production of serial behaviour involves the parallel activation of a set of actions, which together comprise some "chunk", so that responses are internally activated before being externally generated. This activation, in itself, does not contain the serial ordering of the actions. Superimposed on this activation is some kind of independent ordering system, a "schema for action", which selects which response, of those activated, to produce at which time.

This standpoint was inspired by the psychophysical evidence gathered in speech and typing. These studies revealed that before the internal or overt articulation of a sentence, an assemblage of words is partially prepared (Thorson 1925). Additionally it was shown that the most frequent typing errors are those of anticipation i.e., the misallocation of the words in the text, contrary to or different from where they are normally expected (Ruhl 1935). Surveying the then available ideas, Lashley concluded that chain theories are untenable, and furthermore, neither neurosciences nor psychology had much insight to offer into the problem.

Unfortunately, Lashley was able to progress no further, writing that,

"*Indications ... that elements of the [sequence] are ... partially activated before the order is imposed upon them in expression suggest that some scanning mechanism must be at play in regulating their temporal sequence. The real problem, however, is the nature of the selective mechanism by which the particular acts are picked out in this scanning process and to this problem I have no answer*"

There has been a wealth of research since, ranging from behavior and computational models (Rumelhart & Norman 1982; Houghton 1990; Lessard et al. 1992; Hurlstone et al. n.d.) to neural recordings (Averbeck et al. 2002; Rhodes et al. 2004; Bohland & Guenther 2006; Grossberg 2013) lending credence to Lashley's hypothesis on co-temporal activation of action representations.

Taken together the outcome of these studies could be interpreted as the ability to preplan the upcoming action elements in advance, or in parallel with executing the previous ones, to maintain a faster and smoother flow in the overall sequential movement. This ability would in turn result in the emergence of an secondary component to learning in addition to improved S-R mapping. Reviewing the effects of practice on performing random sequences across the literature, this component of learning seems to express, only when the action cues in the sequence are fully visible at the beginning of the trial (Wiestler et al. 2014), but not when the cues are revealed on-by-one (Nissen & Bullemer 1987; Keele et al. 2003b; Haider et al. 2018; Verwey et al. 2014; Rhodes et al. 2004), suggesting that the motor system utilizes the additionally present information to benefit performance.

However, the way in which, and the extent to which the motor system utilizes in advance-information regarding upcoming actions to preplan future movements remains poorly understood. The main literature looking into the extent to which in-advance information affects performance come from reading and speech studies. In a seminal study McConkie et. al. (McConkie & Rayner 1975) reported that the perceptual span in reading is asymmetric, with considerably more information obtained from the right of eye fixation location than from the left. This finding, clearly point to the fact that in-advance information is used to preplan future utterances. Furthermore, it suggests that more effort in concentrated on planning future words, rather than the immediately upcoming one, indicating that it has been preplanned in advance, while reading previous words.

This finding was validated by a word-masking study (Rayner et al. 1980), stating that the reader takes advantage of up to 15 letters (~ 2-3 words) ahead, while reading never-seen-before text. Also interestingly, it has been shown that this perceptual span in beginning readers is slightly smaller than the perceptual span of skilled readers i.e., 11 character spaces to the right of fixation (Rayner 1986). This study suggested that beginning readers devote

more of their attention to the foveally fixated word, rather than the upcoming words compared to more proficient readers, but their perceptual span appears to be asymmetric to the right of fixation as is the case for skilled readers. The results of the experiments also indicated that the size of the perceptual span is variable and can be influenced by the difficulty and familiarity of the text.

In the context of movement planning, it was recently suggested (but not tested) that the planning horizon i.e. the timescale (or number of actions into the future) over which future actions are aggregated and preplanned, should be influenced by experience, such as the stability or volatility of the task environment. In other words, the structures of the environment should be reflected in the representations that are learned (Momennejad et al. 2017). For instance, in more stable environments (e.g., previously learned action sequences), it may be rational to cache representations with multi-step contingencies over longer planning horizons. Whereas in volatile environments, where transition contingencies change frequently (e.g., random action sequences), it would be counterproductive to cache long-term contingencies, but rather preplan more prudently for a smaller or shorter horizon of actions (Sutton 1990).

This sort of cost-effective planning strategy is supported by another recent study, which frames motor planning in terms of an optimal control problem, where computational complexity grows exponentially with the horizon of preplanning (Ramkumar et al. 2016). This study suggests that to learn quickly and efficiently, long actions are broken down into small “chunks” at first to limit the cost of computation. However, practice reduces the load of these computations, allowing for longer chunks to be preplanned. However, in this study the focus was on simple center-out reaching movements, over which monkeys where fully trained.

In real-life actions however, we are mostly faced with unpredictable situations with uncertain upcoming courses of action. Still, humans do improve at performing in uncertain task environments throughout life. Given that the focus in most motor learning studies is on a small subset of trained sequences, the sequence non-specific or general effects of learning remain under investigated.

1.3 The current study

In this study, we set out to examine the span of motor preplanning i.e., the preplanning horizon in the context of general learning in a finger sequence task. Furthermore, we investigated whether the size of the preplanning horizon is affected by learning.

To this end, we designed a novel finger task, which contains the classical DSP design and the full-view design (Wiestler et al. 2014) as the two extreme ends of a unified paradigm; i.e. finger sequence production with varying viewing window sizes of in-advance information. In this sense, DSP would be equivalent to a window size of 1, where participants are only able to see on element ahead of their press position in the sequence. At the other extreme, full-view would be the full sequence window size, where all the elements in the sequence are shown at once.

We utilize this design to manipulate the amount of information provided to the motor system regarding future elements of the sequence. This in turn will allow us to examine the motor planning horizon into the future over the course of learning, as participants undergo a five-session training program.

Furthermore, in this study we tracked and recorded eye movements as an additional readout of the motor preparatory process. To this end, we examined the distance between the fixation position of the eye in the sequence and the digit currently being pressed, as a measure of hand-eye coordination. This is substantiated in the studies highlighting the importance of interconnected functions of the eye and hand and their relevance in movement preparation, predictive motor control as well as decision making (Rizzo et al. 2017; Johansson et al. 2001; Vieluf et al. 2015; Foerster & Schneider 2015; Engbert et al. 2002; Carpenter & McDonald 2007). Specifically, gaze control seems to contribute to the development and maintenance of sensorimotor processes that support predictive control of movement (Johansson et al. 2001). Furthermore, in the context of sequence learning. it has been shown that oculomotor information regarding the sequence can be stored in memory and enhance response production (Vieluf et al. 2015).

Our results suggest that the motor system indeed utilizes in-advance information to preplan actions into the future. Interestingly, our results also suggest a modulatory effect of viewing

window size on the beneficiary manifestations of learning, i.e., learning benefits performance more for larger window sizes. Furthermore, we show that the preplanning horizon expands as a result of learning, meaning subjects improve their ability to effectively utilize the provided information regarding upcoming presses. Finally, we propose a drift-diffusion-based race model to suggest a phenomenological explanation underlying these effects.

2 Methods

2.1 Participants

Fifteen right-handed neurologically healthy individuals (average age 26, 6 males) were recruited for this study. Each individual participated in 5 sessions of training (1.5~2 hours each, on 5 separate days). All participants provided written informed consent and were naive to the purposes of the study. Experimental methods were approved by the Western University Research Ethics Board.

2.2 Apparatus

Participants had their right hand on a custom-made keyboard (Fig. 1A), with a force transducer (Honeywell FS series) mounted underneath each key. The keys were immobile and measured isometric finger force production. The dynamic range of the force transducers was 0–16 N and the resolution 0.02 (N). A finger press/release was detected when the force crossed a threshold of 1N. The forces measured from the keyboard were low-pass filtered, amplified, and sent to PC for online task control and data recording.

Additionally, we recorded monocular left eye movements, all throughout the study using an SR Research EyeLink 1000 desk-mounted eye tracker. Eye movements were recorded at 500Hz sampling rate. Participants sat approximately 40cm away from a 21” screen. The numerical stimuli were shown in white against a black background, horizontally aligned in a single line and spanned ~36˚ of the visual angle.

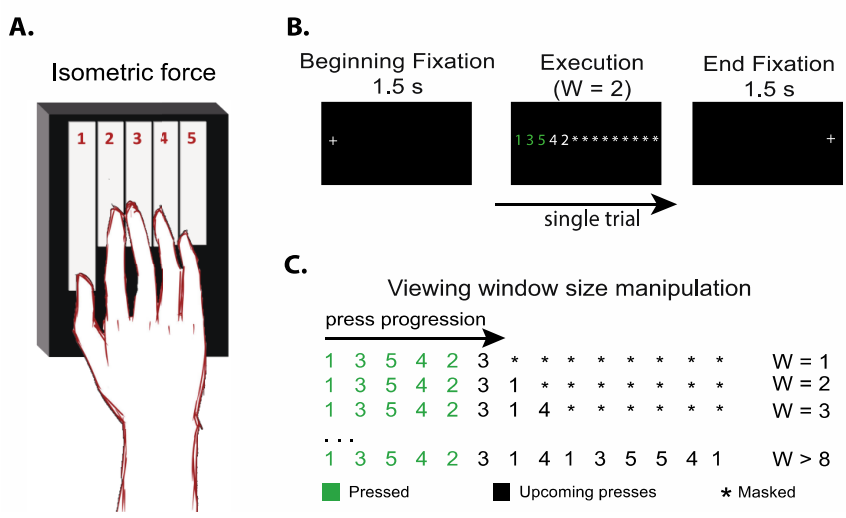

Figure 1: Apparatus and stimuli. ***A*****, participants generated isometric finger presses on a custom-built keyboard with force transducers within each key.** ***B*****, participants had to respond to sequences of numerical stimuli (1-5 for thumb-pinky respectively), quickly and accurately from left to right. At the beginning and end of every trial, a fixation cross appeared on the locations of the first and last digit in the sequence respectively.** *C.* **on every sequence trial a randomized fixed window size (W) of digits ahead of the current press position were visible to the participant, and the rest were masked (W ∈ {1, 2, 3, 4, 5, 6, 7, 8, 13}).**

2.3 Experimental design

During a training session participants sat in front of a computer screen, with their right hand on the keyboard, and their chin placed on the eye tracker chin rest. The task was to make keypresses in response to numerical sequences shown on a computer screen (1-5 corresponding to thumb-pinky respectively) from left-to-right as quickly and accurately as possible (Fig. 1B). At the beginning and end of every sequence trial, a fixation cross (1.5 seconds) was presented in location of the first and last digits in the sequence (far-left and far-right) respectively. These fixation locations were used to apply a trial-by-trial calibration and thus account for possible drifts and calibrate the eye-to-digit location mapping on a single trial basis.

On every given sequence trial, only a fixed number of digits (viewing window size, W) ahead of the press position were revealed to the participants, while the rest were masked with

asterisks (Fig. 1C). The masked digits were revealed as the participant proceeded with the presses. W varied within the domain of {1, 2, 3, 4, 5, 6, 7, 8, 13}, and was randomized across trials within every block.

With every press subjects received visual and auditory feedback. The white cue turned either green or red accompanied with the corresponding sound feedbacks for correct and incorrect presses respectively. With the completion of every trial, participants received points based on their performance. A trial was considered an error if it contained one or more incorrect presses, for which participants received zero points. Correct sequences were rewarded with at least 1 point. If the sequences were performed faster than certain thresholds the points for a given trial could go up to 2 or 3. The threshold for receiving 2 and 3 points were designed to get increasingly difficult adjusting to every subject's speed throughout training. At the end of each block, participants received feedback on their error rate, median sequence execution time, total points obtained during the block, and total points obtained during the session. Subjects were asked to maintain error rate below 15% per block.

On every training session (between 1.5 to 2 hours) subjects were trained for 8 blocks of 14-digit-long sequences with 27 trials per block, as well as 3 blocks of short segments of lengths 3 and 4 (triplets and quadruples respectively, Fig. 2A) with 60 trials per block. One-third of the trials in every sequence training block were random, and were generated by random shuffles of digits 1-5 (Fig. 2B). The remaining 2/3 of the trials were structured sequences (Fig. 2B). Each participant was assigned three unique triplet (T) as well as three unique quadruple (Q) segments, which they were trained on, during the short segment blocks. These short segments were concatenated to form the structured sequences. Every structured sequence consisted of 4 segments, in arrangements of QQTT or TQTQ. The T and Q segments were randomly shuffled to form various structured sequences.

The size of the viewing window (W) was varied randomly within each sequence training block. However, in the segments training blocks, all the digits were always visible to the participants. The purpose of Including the segments training block, was to study the effect of the amount of information regarding up-coming actions in performance unfamiliar and partially familiar sequences (random and structured sequences respectively). The order of sequence training and segment training blocks were reversed only for the first session,

meaning that the participants were naïve to the segments, when performing the structured sequences on session one (Fig. 2A).

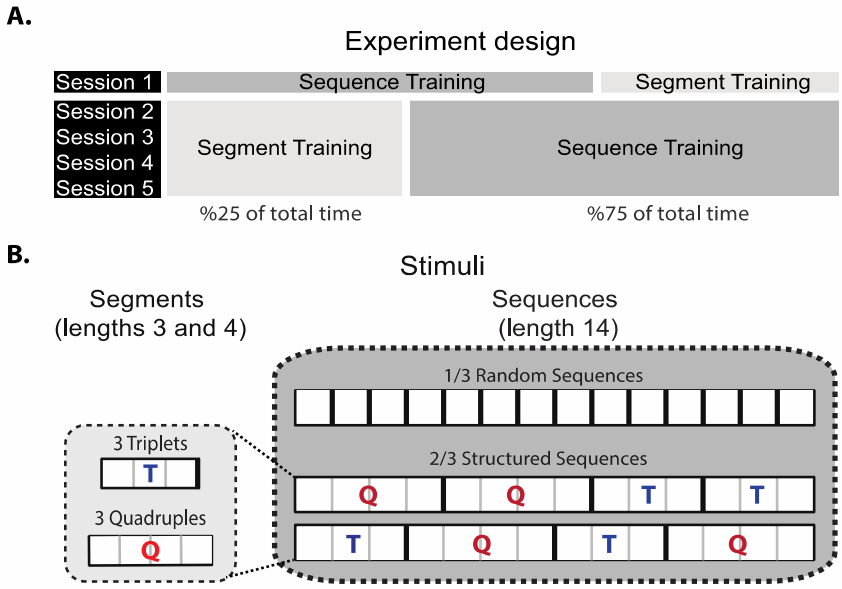

Figure 2: Experimental design. ***A*****, each training session consisted of 8 sequence training as well as 3 segment training blocks. On the first session sequences were trained before segments. From session two onward, this order was reversed.** ***B*****, Every sequence training block consisted of 1/3 random sequences, generated by random shuffles of digits 1 to 5, as well as 2/3 structured sequences. Every individual was assigned a unique set of 6 short segments which they were trained on starting at the end of the first session. These short segments were concatenated to form various 14-digit structured sequences. W randomly varied within each sequence training block.**

2.4 Finger press data analysis

The speed and accuracy of sequence production were used to measure the effect of practice throughout the 5-day training program. This decision was due to the fact that on any given trial, participants were rewarded based on accuracy and speed of sequence production with points. The time taken into account for pointing was the time between making the first press, to making the last press in the sequence. For a press to register, the force applied on the key by the corresponding finger had to cross the threshold of 1.5 Newton.

The main measures taken into account are as follows:

Initial reaction time (RT): the time from the stimulus onset on the screen to making the first press, i.e., the first pressed key crossing the 1.5 N threshold.

Sequence completion time (ET): the time between making the first press in the sequence, to making the last press in the sequence, i.e., the time between the first key crossing the threshold, to the last key crossing the threshold.

Inter-press interval (IPI): the time between every two individual presses in the sequence, i.e., the time between two consecutive keys crossing the threshold.

2.5 Eye movement data analysis

In this study, eye movements where used as a proxy to provide a read-out of the higher-order motor preparation processes. To this end, it is necessary to be able to estimate the digit on which the eyes fixate at any given time throughout sequence execution. $D_{current}^{t,b}$ is the digit on which the eye is currently fixated in trial t and block b, and is acquired by mapping the calibrated current position of the eye in tracker units ($X_{current}^{t,b}$) to the digits on the screen.

$$D_{current}^{t,b} = \frac{X_{current}^{t,b} - X_{startFix}^{b}}{P_x^b} \qquad (1)$$

where $X_{current}^{t,b}$ is the eye's current horizontal position in trial t and block b in eye tracker units. P_x^b is a constant per block of trials, used to convert eye tracker units to digit positions on the screen, calculated as per (2),

$$P_x^b = \frac{X_{endFix}^{b} - X_{startFix}^{b}}{14} \times d \quad , \quad d = 1.5\ cm \qquad (2)$$

where d is the distance between each pair of digits on the screen in centimeters. $X_{startFix}^{b}$ and X_{endFix}^{b} are the median horizontal position of the eye during the 1.5 sec fixation cross periods at the beginning and end of all the trials within block b respectively, calculated as per (3) and (4).

$$X^{b}_{startFix} = median(\{X^{t,b}_{startFix} \mid t \in [block\ b]\}) \quad (3)$$

$$X^{b}_{endFix} = median(\{X^{t,b}_{endFix} \mid t \in [block\ b]\}) \quad (4)$$

$X^{b}_{startFix}$ and X^{b}_{endFix} are in eye tracker units and are kept constant for all the trails within every block (27 trials and ~10 minutes per block). Within every block, participants were instructed to not remove their chin from the eye tracker chin-rest and to not move their heads.

3 Results

Because we are especially interested in sequence-unspecific, general effects of learning, only the data acquired from the long random sequences are going to be discussed in this paper. The data regarding the short segments, as well as the structured sequences will be presented elsewhere.

3.1 The motor system utilizes in-advance information to preplan actions

First, we tested whether and how the amount of information regarding the upcoming presses in the sequence affects performance. We manipulated the degree of in-advance information provided to the participants by randomly varying the viewing window size (W) from trial to trial within each sequence training block. Sequence execution time (ET) which is the time needed to fully perform a sequence of 14 digits, was used to measure and evaluate performance. The group average of performance on the first day of training in shown in Fig. 3. The error trials (17.6% overall error rate) are excluded from the analysis all throughout the results. ET clearly decreases in trials with larger window sizes. The window size-related changes in performance on day one, i.e., early learning, are substantiated by the highly significant main effect of W on ET in an analysis of variance (ANOVA), $F(8,112) = 89.74$, $p<10e-10$.

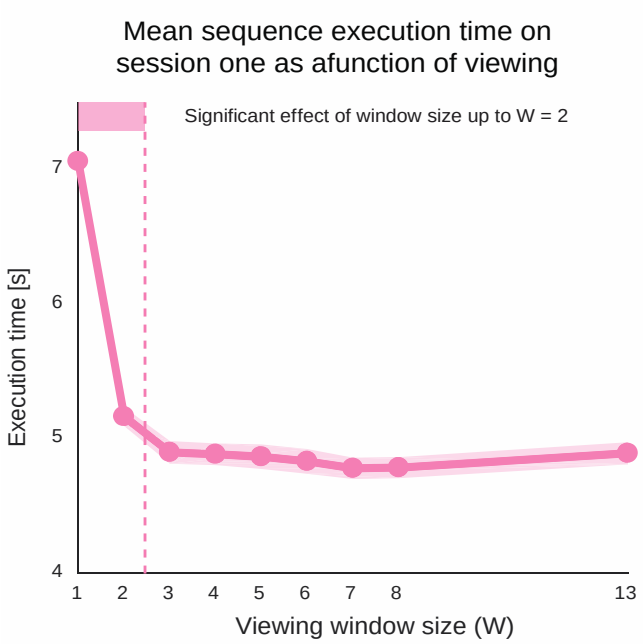

Figure 3: On day 1 of training, performance speeds up significantly in trials with larger window sizes up to W = 2. For window sizes 3 and larger, window size shows no significant main effect on execution time, indicating a preplanning horizon size of 2 digits ahead in the early phase of learning.

Interestingly the beneficiary effects of larger window size on ET seems to plateau well before the full-view window (W=13). To quantify this effect, a number of post hoc F-tests were carried out, where we cumulatively excluded window sizes from the test one by one, in order of size and, starting from W = 1 and repeated the F-test. This procedure was continued until the main effect of W on ET became nonsignificant. The purpose of these tests was to estimate the *preplanning horizon*, defined as the window size larger than which performance does not improve any further. We estimated this value as 2 on the first day of training, since after excluding W = 1 from the test, the main effect of W on ET was still significant ($F(7,98) = 2.87$, $p= 0.009$), however became non-significant with the exclusion of window sizes 1 and 2 ($F(6,84) = 0.87$, $p = 0.5$).

In window size 1 where the next cue is presented only after the execution of the previous cue, there is no possibility of preplanning the upcoming press in parallel with executing the previous. Therefore, participants are forced to cycle through the planning and execution processes of every press in serial order. Thus, the fact that on day 1, performance

significantly benefits from information regarding up to 2 digits ahead of the press position (Fig. 3), suggests that subjects utilize the additional information to preplan their next press in parallel with executing the previous one and hence speed up execution.

3.2 Benefits of learning are expressed more strongly in larger window sizes

Based on our finding that performance improves significantly with larger window sizes, next we asked whether learning affects performance differently depending on the number of revealed upcoming presses. To examine this, we submitted the ET across 5 sessions of training and 9 different window sizes (Fig. 4A) to a within-subject ANOVA. This test revealed a significant interaction effect between window size and training session on ET ($F(32,448) = 3.12$, $p = 0.703e\text{-}09$), indicating that the benefits of learning on performance, are mediated by the size of the viewing window.

To test this effect further, we carried out a series of post-hoc tests, examining the effect of practice on ET within every window size separately. Critically, except for window size 1 (Fig. 4A, W = 1) this analysis revealed a significant effect of training sessions on ET in all other window sizes ($F(4,56) = 13.79$, $p= 0.679e\text{-}09$ for $W>1$). Nevertheless, when comparing performance on day one to the last day of training in a right-tailed paired t-test for each window size individually, we found a reliable reduction in ET even in window size one ($t=3.18$, $p= 0.955e\text{-}05$). Specifically, ET on average decreases by 7.42% from first to last day of training (Fig. 4B, Overall learning shown in black bars) for W=1. This amount of improvement can be attributed to improvement in individual digit-to-finger S-R mappings. However, the learning-related improvements are more highly expressed with larger window size, as verified by the significant main effect of window size on first-to-last-day %decrease in ET ($F(8,112) = 10.42$, $p= 0.791e\text{ -}12$). This finding suggests that although S-R mapping shows improvement over the course of training (W=1), it does not explain the additional effects practice in larger window sizes. Rather these additional learning effects seem to originate from the ability to use the in-advance information more effectively as a result of practice.

Additionally, we looked at the partial effects of learning on performance by examining the %decrease in ET from day 1 to 3 (initial phase of learning, Fig.4B, shown in light gray bars),

as well as day 3 to day 5 (final phase of learning, Fig.4B, shown in dark gray bars). As expected, performance improved most in the initial as compared to late phase of learning ($F(1,14) = 5.01$, $p = 0.041$). Nevertheless, the main effect of window size on the amount of improvement is highly significant even in the late phase of learning ($F(8,112) = 6.52$, $p = 0.586e\text{-}08$). This finding further emphasizing the critical role of in-advance information towards taking full advantage of practice benefits throughout training.

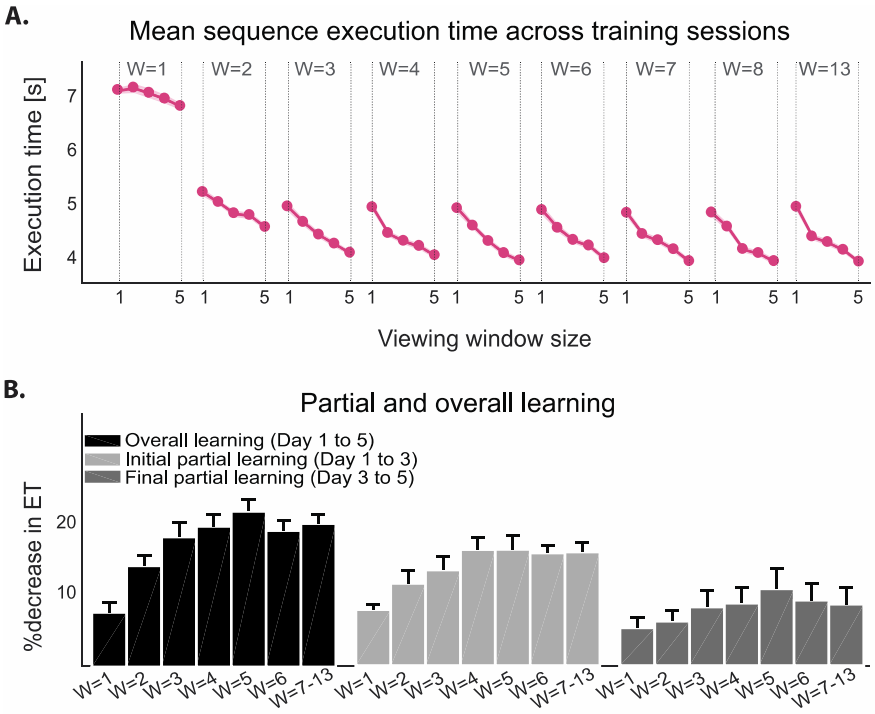

Figure 4: The effects of practice on performance are manifested more strongly in larger window sizes. ***A*****, execution time decreases with practice in all window sizes, both partially, i.e., day to day, and overall.** ***B*****, the beneficiary effect of learning on performance is modulated by two main factors *a)* the viewing window size, i.e., trials with larger window sizes, show a stronger manifestation of learning effects both on the partial and overall levels, and *b)* stage of training, i.e., performance benefits from the same amount of practice to a larger extent during the early portion of learning (day 1 to 3, light gray), as compared to the late portion of learning (day 3 to 5, dark gray).**

3.3 The preplanning horizon expands as a result of learning

Given that performance improvements are more pronounced for larger window sizes (Fig. 4), we asked whether these changes are mediated by an increase in the preplanning horizon. This seems potentially likely, substantiated in the highly significant interaction effect between W and training session on ET ($F(32,448) = 3.12$, $p = 0.703e\text{-}09$). To investigate this further, we examined the preplanning horizon at the group and individual levels, in a series of post hoc tests.

First, we determined the group-level preplanning horizon on day 5, using the same method explained in section 4.1. Previously we estimated the preplanning horizon to be 2 digits ahead of the press position in the sequence on day 1, as the effect of window size on ET became non-significant after eliminating W = 1, 2 from the F-test (Fig. 3). Interestingly, and by the same token, this horizon increases to 3 digits ahead of the press position on days 2 and 3 (mid-training) and finally to 4 on days 4 and 5 (late training, Fig. 5A).

To allow for a statistical comparison, we estimated the preplanning horizon size on the individual level (N = 15), in early (day 1), mid (days 2, 3) and late (days 4, 5) learning phases. The main motivation for this analysis was to account for the high level of inter-subject variability in behavior, by comparing every individual to him/herself in different learning phases. Thus, for each subject and phase of learning, the preplanning horizon was defined to be the largest window size where the ET is still significantly larger than the mean of ET over all larger window sizes pooled together, in a right-tailed paired t-test.

Next, we compared the individually calculated preplanning horizons in a within subject ANOVA, with the three learning phases as factors. This test revealed a significant main effect of training phase on horizon size ($F(2,28) = 7.53$, $p = 0.002$), further validating the extension of estimated preplanning horizon as learning progresses, despite the inter-subject variability. The smaller estimated horizon sizes obtained on the subject level, can possibly be explained by the assumption of normality in the utilized tests, i.e., the data has a distribution closer to normal on the group level compared to the individual-level.

Nevertheless, this finding provides further evidence that with practice, participants learn to utilize the supplied information in an increasingly efficient manner, which results in better performance for larger window sizes. This in turn indicates that in addition to individual S-R mappings, general learning provides the motor system with a more effective way of orchestrating the planning and execution processes provided the possibility (for W > 1). However, for W = 1 where the task setup dictates serial progression of planning and execution, or for window sizes smaller than the preplanning horizon size, the motor system loses the opportunity to benefit from the additional component of general learning either fully (for W = 1), or partially.

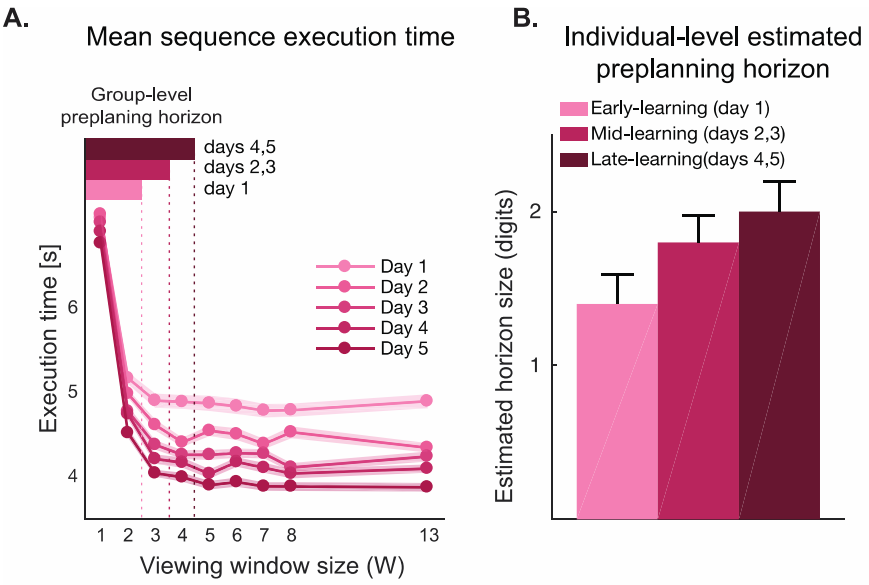

Figure 5: the preplanning horizon expands with learning. ***A.*****, regardless of the phase of learning, performance improves significantly with larger W. The improvement in performance plateaus after a certain window size (the preplanning horizon). At the group level, the W after which performance does not improve further is W = 2 on day 1, and W = 4 on day 5.** ***B.*****, also at the individual level (N = 15), the preplanning horizon shows a significant monotonic increase as learning progresses.**

3.4 The importance of initial planning

Our results clearly point to a robust and positive relationship between the amount of in-advance information regarding upcoming presses and performance. We also show the same positive relationship between window size and manifestations of learning. We attribute these

positive effects to the possibility of preplanning additional actions into the future in larger window sizes. To investigate this claim, we examined the initial response time (RT), i.e., the time from stimulus onset, to making the first press in the sequence (Fig. 6). RTs are known to be closely tied to the mental processes yoked to movement preparation (Haith et al. 2015), therefore we expected to find larger RTs for larger window sizes, as an indication of more extensive preplanning. Interestingly, the data validates this expectation, substantiated in the significant effect of window size on RT ($F(8,112) = 3.53$, $p = 0.001$). This is consistent with a critical role of effective preplanning in optimizing performance.

Next, to gain more insight about the mechanism and extent of preplanning throughout sequence execution, we examined the individual inter-press intervals (IPIs). We expected to find all the individual inter-press intervals (IPIs) within a sequence to fall within an insignificant distance of the first IPI. This would validate one pivotal assumption: that the planning and execution processes progress at the same rate, so that the planning process is always a fixed number of digits ahead of the execution process (the preplanning horizon size). However, the data renders this assumption inaccurate.

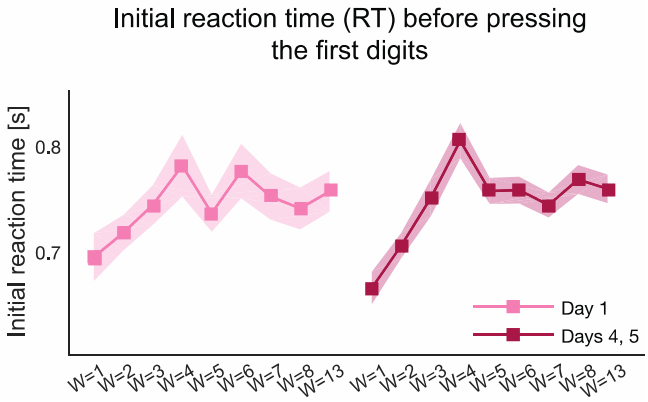

Figure 6: Initial response time increases for larger window sizes, indicating more extensive preplanning considering the close tie between RT and movement preparation

We examined individual IPIs durations, with respect to their placement within the sequence, i.e. IPI_{1-13} for 14-press sequences (Fig. 7A). Importantly, we found a highly significant effect of IPI placement within the sequences on IPI duration ($F(12,168) = 23.22$, $p < 10e\text{-}10$). Specifically, we found that the initial (IPI_1) as well as final IPIs (IPI_{13}) are consistently performed significantly faster than the middle IPIs, and this is regardless of the stage of

training or the viewing window size. This is a critical finding, since it potentially suggests that the dynamics of the interplay between the execution and planning processes vary between different stages of sequence production.

We attribute the fast IPI at the end of the sequence, to the biomechanical properties of the hand. This assumption originates from the fact that there are no upcoming presses, thus the hand does not need to hover above the keyboard for the next movements. This provides more comfort and speed in making the last press. However, the same logic does not apply to the high-speed initial IPI. Interestingly, a highly significant negative correlation between RT and the duration of the first IPI (IPI_1) was found on the late learning phase (days 4 and 5, ρ = -0.35, p=0.304e-06). This negative correlation is present in the early learning phase as well, although insignificant (day1, ρ = -0.15, p =0.076). This finding suggests that not only preplanning benefits performance, but also the extent to which upcoming presses are preplanned (as reflected in RT) mediates the speed of the present press (as reflected in IPI_1). With this mind, the fact that the IPIs towards the middle of the sequence get substantially slower compared to the initial IPIs, potentially indicates that the motor system takes the most advantage from the provided in-advance information at the beginning of the movement.

To investigate this further, we examined eye movements. If it is the case that better performance in initial IPIs (Fig. 7A) is due more effective preplanning we expect to find that the eyes fixate further ahead of the press position when making the first press, compared to the middle presses in the sequence. Furthermore, and by the same token, we would expect to find that for larger window sizes the eyes would generally fixate further ahead relative to the digit being pressed.

Fig. 7B shows the distance between the eye-fixated digit relative to the digit being pressed within the sequence, at the time of 14 presses for 9 window sizes. As anticipated, the eye fixation position is furthest ahead of execution at time of making the first press. This distance then reduces towards the middle of the sequence. Finally, towards the end of the sequence the eye fixation position consistently falls behind the execution and stops before the end of the sequence.

The modulatory effect of the order of the digit being pressed in the sequence on eye-press relative distance is verified by the highly significant main effect of press number (F(13,143)

= 41.31, p = 0.00). Given that the sequences being discussed are all random, participants cannot benefit from retrieving information from memory. Thus, to make the correct presses, subjects had to look at the numbers on the screen and respond with the appropriate fingers. Thus, if the eyes are fixated ahead of the digit being currently pressed, we find it safe to take that as a sign of preplanning upcoming presses. It is worth noting that the full 14-digit sequence on the screen spans approximately 36° of the visual angle and therefore every given pair of sequential cues are approximately 2.5° apart. It has been shown that during reading, information within 2° (approximately 6-8 characters) of the point of fixation is processed in foveal vision, while information up to 5° of visual angle benefits from parafoveal preview (Engbert et al. 2002). Thus, the possibility that up to two digits ahead of the fixation position can be the digit currently intended for preplanning is not far from reality.

Also as expected, the eyes fixate further ahead of the press position in larger window sizes, substantiated in the robustly significant main effect of window size on eye-press relative distance ($F(8,88) = 13.15$, $p = 0.255e\text{-}13$). Taken together these findings not only suggest that the optimized performance in larger window sizes is indeed due to more extensive preparation of future presses, but also emphasize the critical importance of initial preplanning.

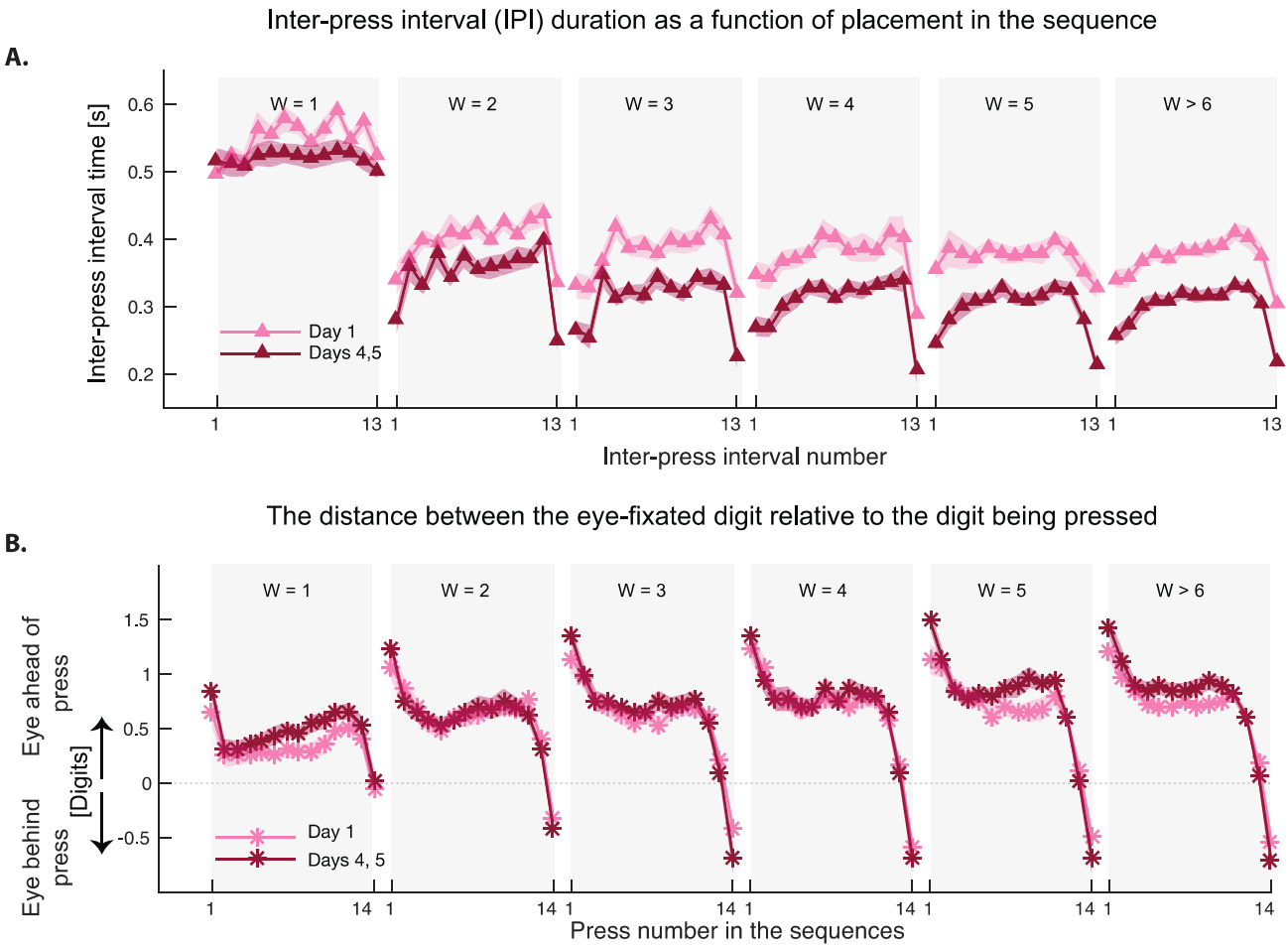

Figure 7: Inter-press intervals and eye-press relative distance show indications of more effective preplanning in larger window sizes *A.* **IPI curves as a function of IPI number in the sequence (1-13), for different window sizes (data relative to windows larger than 6 are pooled together). Initial as well as final IPIs are substantially faster than middle IPIs, indicating the varying dynamics between the motor preparation and execution processes throughout sequence production.** *B.* **the relative distance between the eye-fixated digit and the digit being executed, at the time of 14 presses for different window sizes (data relative to windows larger than 6 are pooled together). Except for the last two digits in the sequence, the eyes are always fixated head of the press, being the furthest ahead at press 1. The eye-press relative distance expands even further in larger window sizes indicating the ongoing preplanning process.**

4 The race model

4.1 The single finger press race model

Each individual finger press can be thought of as a single action selection process followed by action execution. Each selection process can then be modeled as a motor decision, resulting from a competitive race between five alternative responses, associated with fingers thumb to pinky (Rowe et al. 2010; Kornysheva et al. 2013; Churchland et al. 2008) (Fig. 8).

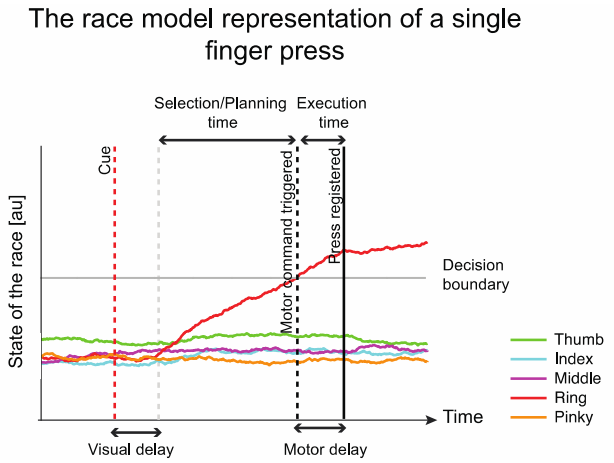

Figure 8: Each individual finger press is modeled as a competitive race between 5 alternative responses. With the onset of the cue (here the digit 4, corresponding to the ring finger), and after a fixed sensory delay, the process of evidence accumulation begins, resulting in the forth option in the race drifting closer to the fixed decision boundary. Once a winning option reaches the decision boundary, a motor decision is issued, i.e., motor planning is completed. Finally, the motor command is triggered and movement is initiated after a fixed motor delay.

In this sense, the process of making a single finger press is as follows. After a fixed visual sensory delay (considered 100ms in the model) from the onset of the visual cue, the temporal accumulation of evidence starts in favor of the instructed finger. The accumulation process continues until there is a winner in the race, i.e., one of the five options in the race reaches the fixed decision boundary B. At this time, a motor decision is issued. The duration of the time between the cue onset and the issuing of the decision, represents motor planning. Thus,

in this model, we do not distinguish between movement selection and planning, but rather hypothesize that the brain prepares multiple actions at the same time (Cisek & Kalaska 2010). Subsequently, depending on the winning option in the race, the appropriate motor command is triggered and finally, after a fixed motor delay (considered 120ms in the model) the press is registered. This planning / selection process is formulated through a simple accumulator model (McKoon 2008) as per:

$$x_{i+1}^{f} = x_i^{f} + \theta S_i + \epsilon \qquad f = 1 - 5 \qquad (5)$$

where x_i^f is the state of the race for finger f (1-5) at time i. S_i is the state of the visual stimulus at time i, defined as an indicator vector of length 5, where only the element corresponding to the instructed finger is set to one. S_i is multiplied by the accumulation rate θ, which translates into the slope with which the cued option (the ring finger in Fig. 8) approaches the decision boundary. Finally, ϵ is the additive independent noise drawn from a normal distribution at any given time i. This single press race model was then used as the building block to model the performance in random sequences

4.2 The sequential race model

Executing a random finger sequence involves making an ordered series of individual presses in response to independent sequential cues. We thus used a series of 14 independent single press races ($(Eq. 5)$, Fig. 8) to model the performance in 14-digit random sequences.

Importantly, this implementation provides the sequential model with the flexibility to represent both serial and parallel planning / execution in a unified framework. This is critical, since in the task, for window size 1, each cue in the sequence is revealed only after the response to the previous cue has been executed (Fig. 1). Consequently, there is no possibility of planning the upcoming press(es) in advance. Thus, the motor system cycles through the planning and execution processes of every press in serial order. This results in the accumulation of evidence for each press to start only after the current press has been initiated (Fig. 9 A and D).

However, for window sizes larger than one, cues regarding the upcoming presses are available. As supported by the data, the motor system utilizes the supplied information to

optimize performance (Fig. 3 and Fig. 4 A), indicating that the future actions are prepared for execution in parallel with executing the previous ones. This indicates that depending on the window size and the preplanning horizon, the accumulation of evidence for multiple races are carried out in parallel with each other (Fig. 9 B, C, E and F).

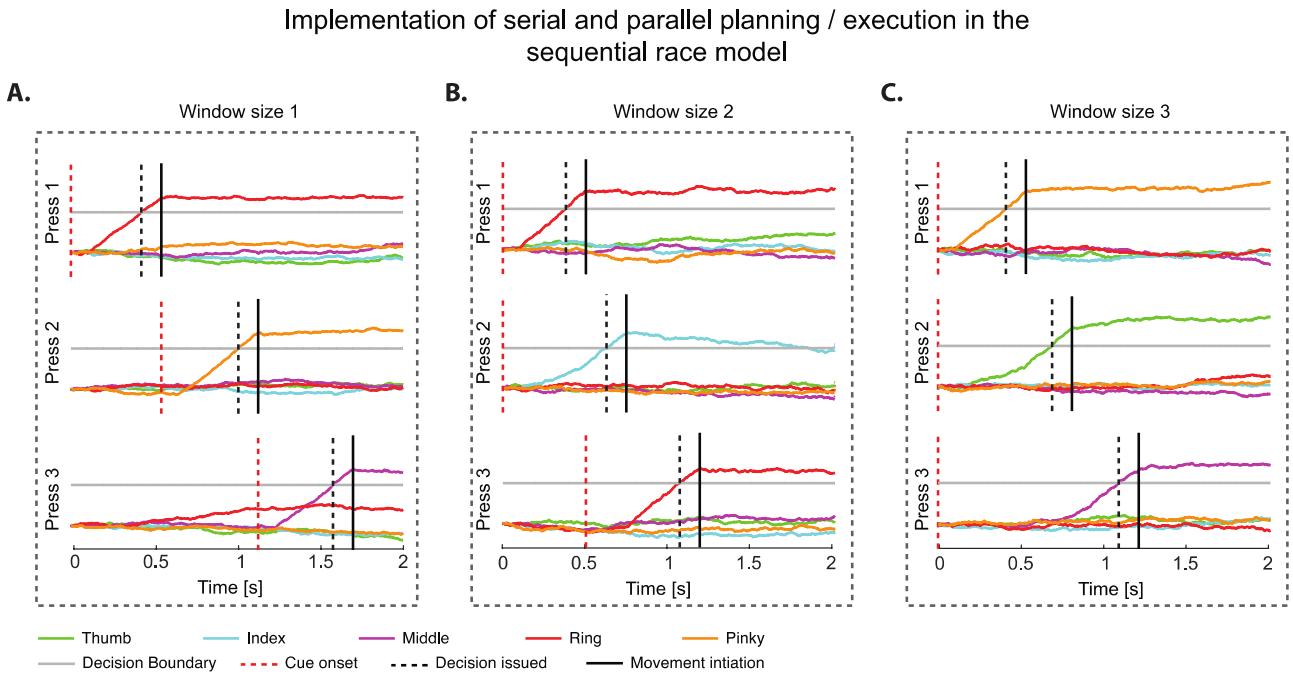

Figure 9: The sequence representation of the race model allows for both serial and parallel planning/execution. ***A.*****, in window size of one in the task, the next cue in the sequence is revealed after the response to the previous cue. This dictates that the motor system plans and subsequently executes each individual finger press in serial order.** ***B.*** **in window size 2 the subject is always allowed to see one digit ahead of the current press position in the sequence. Thus, the motor system has the possibility to utilize the additionally supplied information to preplan one digit ahead of the immediately upcoming press. Hence, the accumulation of evidence for the first two presses in the sequence start simultaneously.** *C.* **similarly in window size 3, two digits ahead of the current press position are revealed at any given time. Therefore, evidence accumulation for the first three cues in the sequence start simultaneously at the beginning. Note that the accumulation rate for the cues further away from the immediately upcoming press, get increasingly slower.**

The sequential race model is parametrized as per,

$$x_{i+1}^{f,p} = x_i^{f,p} + \lambda_p \theta S_i + \epsilon \qquad (6)$$

where $x_i^{f,p}$ is the state of the pth race for finger f (1-5) and press p (1-14) at time i. S_i is the state of the visual cues for at time i, defined as a binary matrix of size 5×14 for the five fingers and 14 presses in the sequence. Thus, similar to the single press model $(Eq. 5)$, each column $S_i^{(p)}$ is an indicator vector of length 5, specifying the cued finger for press p. In accordance with the viewing window size (W), W-1 cues ahead of the immediately upcoming press are revealed. Thus, at any given time i, W-1 columns ahead of the current press are filled with their corresponding cues in the S_i matrix. The stimulus matrix is then multiplied by the accumulation rate θ, scaled by the preplanning weight λ_p.

The λ_p weights are meant to control the parallel evidence accumulation rates for window sizes greater than 1. Note that when performing a sequence, the order of correct finger presses in the sequence have to be maintained according to the instructed cues. Therefore, when preparing multiple actions in parallel, it is crucial for the evidence accumulation rate to monotonically decrease for cues further away from the immediately upcoming press ($\lambda_1 = 1, \lambda_{p>1} < 1$). This will insure that the future races do not reach the decision boundary B, before the termination of the current race. As a result, the order of sequential presses will be preserved as cued (Fig. 10).

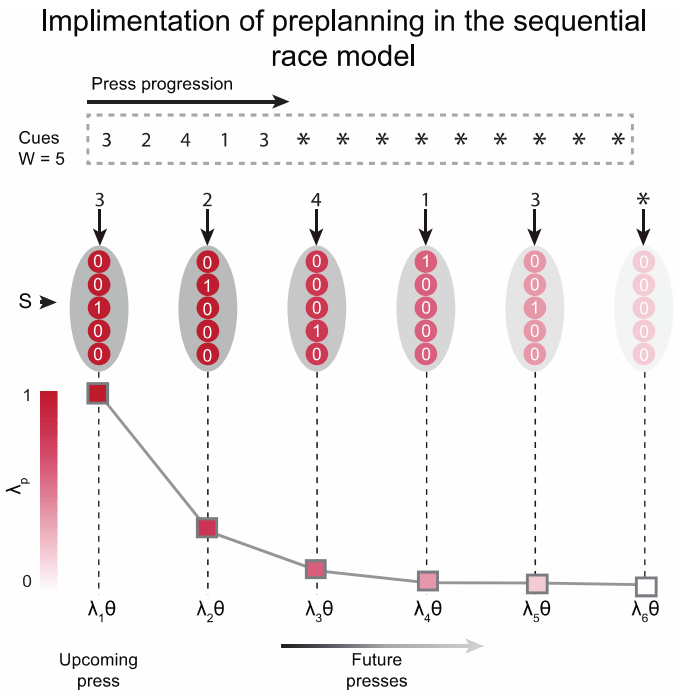

Figure 10: The accumulation rate of evidence for the future presses in controlled by the preplanning weights $\boldsymbol{\lambda_{1-p}, p = 1 - 14}$. A maximum weight of 1 for the immediately upcoming press, ensures that the next press to make is the first to complete its corresponding race and reach a winning option. The further a press from the next press in line, the smaller the corresponding preplanning weight. Once a press has been initiated, the values of the $\boldsymbol{\lambda}$ vector are shifted one ahead in the sequence, allowing for preplanning of the future away presses.

4.1 Fitting the sequential race model

The sequential race model was optimized to fit the sequence execution times (ET, Fig. 11 B) as well as the inter-press intervals (IPIs, Fig. 11 C and D) for window sizes 1, 2, 3, 4, and 5-13 pooled together. Thus, the objective function to be minimized was defined as the sum of mean squared-errors (MSE) calculated between the two vectors of actual and predicted values as per $[ET_{1,2,3,4,5-13},\ ET_1 - ET_2,\ ET_2 - ET_3,\ ET_3 - ET_4,\ ET_4 - ET_{5-13},\ IPI_{1,2,3,4}]$. Including the difference between the ETs of consecutive window sizes, i.e., $ET_W - ET_{W+1}$ in the objective function, had the benefit of forcing the model to keep the ETs monotonically decreasing for increasing window sizes. Furthermore, IPIs later than 4th were not included in the objective function since after the initial speed up (Fig. 7 B) the

magnitude of the IPIs tends to stabilize from the 3rd or 4th value onwards. Hence, including further IPIs would inflate the MSE value, without benefitting the optimization any further.

For the optimization, we used the Nelder–Mead (NM) heuristic algorithm (Nelder & Mead 1965), implemented in the Matlab function, *fminsearch*. The following parameters were included in the optimization (see $(Eq. 6)$); the evidence accumulation rate (θ), the magnitude of the decision boundary (B) and the elements 2 to 5 in the preplanning weight vector (λ_{2-5}). $\lambda_1$is set to 1, and furthermore, planning weight values for $\lambda_{p>5}$ were set to 0. This decision is justified by the fact that even in the late phase of learning, the preplanning horizon size was estimated at maximally 4 digits ahead of the press position (see Fig. 5). This suggests that the information regarding the cues further than 4 digits ahead, is likely not utilized by the motor system. Importantly, we expected the values of λ_{2-5} to come out as monotonically decreasing, allocating a smaller preplanning weight to the cues future into the future (Fig. 10).

The optimization was carried out for the early and late phases of learning separately, i.e., data from day 1 and days 4 and 5 respectively. The parameters included in the optimization process, as well as the structure of the model, were kept constant for both learning phases. The data from all the window sizes were submitted to the optimization algorithm together. However, it is important to note that not all the optimized parameters contribute to fitting the data from different window sizes equally. For instance, in window size 1, where planning and execution are carried out serially, the values of λ_{2-5} have no effect on the output of the model. Rather the output is solely determined by the values of the accumulation rate (θ) and the magnitude of the decision boundary (B). For window size 2 however, the output of the model is affected by θ, B as well as the value of the second preplanning weight λ_2, as the cues associated with λ_{3-5} are masked with asterisk and thus cannot be utilized. By the same token, the preplanning weighting parameters affecting the model output for window sizes 3, 4, and 5-13 would be λ_{2-3}, λ_{2-4} and λ_{2-5} respectively.

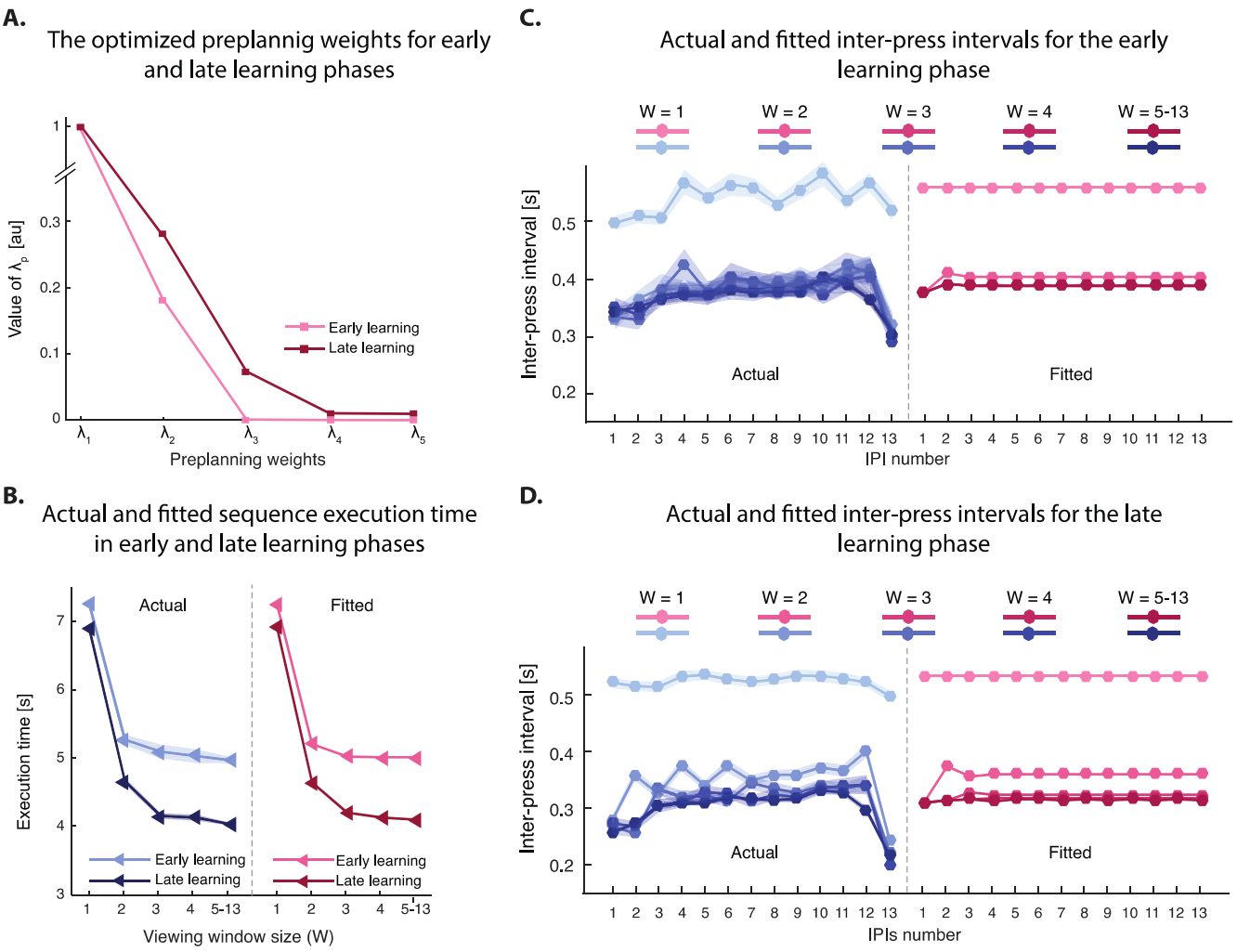

Figure 11: The sequential race model is optimized to fit the data in different window sizes for early and late phases of learning. *A.*, **the optimization, results in monotonically decreasing values for λ_{2-5}. This ensures that the evidence accumulation rate is slowed down for cues further away from the upcoming press, and thus the order of the cued presses is preserved. Furthermore, the preplanning weights are smaller and reach 0 sooner for the early learning phase, compared to late, consistent with the expansion of the preplanning horizon size, supported by the data (see Fig. 5)** *B.*, **the optimized model fits the sequence execution time in early and late phases of learning, by performing increasingly faster for larger window sizes. This effect is mainly due to the parallel accumulation of evidence for an increasing number of cues depending on W (see Fig. 9).** *C.* **and** *D.*, **the model generates the relatively faster initial IPIs in early and late phases of learning respectively. This effect is due to the fact that the simultaneous evidence accumulation processes of the first W presses at the beginning. However, the next cues**

only appear after the execution of the W-1st presses back has been completed. This results in a slow-down and subsequently stabilization of the IPIs.

Optimization resulted in a relatively higher decision boundary B, as well as a higher accumulation rate value θ for early learning compared to late learning. However, we are cautious with interpreting the differences between theses fitted values. Nevertheless, θ and B mainly fall out of the data from window size 1, as they are the only determining parameters for the serial planning/execution (pure reaction mode) condition of the model (see Fig. 4). Furthermore, the optimization also arrives at different preplanning weights λ_{2-5} (Fig. 11 A) for early and late learning phases. Critically but not surprisingly, regardless of the learning phase, the values of the preplanning weights monotonically decrease from λ_2 to λ_5 and they are all smaller than 1 ($\lambda_1 = 1$).

Furthermore, the preplanning weights, λ_{2-5} for early learning are not only smaller than the those of late learning, but they also approach zero faster ($\lambda_{3-5} \approx 0$ in early learning). This is in keeping with the data showing an expansion of the estimated preplanning horizon size with learning (see Fig. 5).

Taken together, given that the preplanning weights λ_{2-5} are estimated by minimizing the difference between actual and estimated IPIs and ETs, lends credibility to the following arguments: *a)* when provided with in-advance information, the motor system preplans actions into the future in parallel with executing the current actions to optimize performance. Otherwise, we would have expected for the optimization process to end up with λ_{2-5} weights close to 0. *b)* the rate at which the evidence accumulates for the future actions, gets increasingly slower for cues corresponding to actions further away into the future. This in turn ensures that the order of the sequential actions is preserved according to cues (see Fig. 10). *c)* as a result of learning, the motor system becomes more efficient in utilizing the in-advance information as reflected in the larger λ_{2-5} weights in late learning compared to early learning.

Additionally, the model replicates the initial speed-up in the IPIs in early and late phases of learning (Fig. 11 C and D). This effect is due to the fact that for window sizes W>1, the evidence accumulation processes regarding the first W presses start simultaneously at the

beginning. Thus, by the time the first race terminates, the evidence accumulation for the next W-1 presses is well progressed, and hence will reach the decision boundary shortly after the first press is made. However, the cues regarding the W+1st press onward, only appear after the execution of the press W-1 before them. Therefore, the evidence accumulation starts relatively later. This trend continues till the end of the sequence, which results in a slow-down and subsequently stabilization of the IPIs.

It is worth noting that the model fails to reproduce the final speed-up in the IPIs (Fig. 11 C and D). We attribute the final speed up to the subject not having to hover the hand above the keyboard for upcoming cues, leading to the last presses being carried out with more ease and comfort. However, at this point the model is purely conceptual with no grasp of the biomechanical properties of the hand. Thus, once the IPIs reach the steady state, they maintain the same speed till the completion of the sequence execution.

5 Discussion

We developed a novel finger sequence production task to examine the span of motor preplanning horizon throughout learning. Participants underwent a 5-session training paradigm, where they learned to map the digits 1-5 to fingers thumb-pinky of the right hand respectively, and execute sequences of numbers quickly and accurately. As one pivotal feature of the task, we randomly varied the viewing window size (W), on a trial-by-trial basis, i.e., on any given trial, subjects were only shown a fixed number of cues ahead of their lastly executed cue in 14-digit random sequences. This manipulation allowed us to examine a) the way in which the amount of in-advance knowledge of future actions affects performance, and b) the way in which learning interacts with this effect.

5.1 Current view on sequence-nonspecific effects of practice

Typically, in finger sequence tasks, subjects are trained on a set of reoccurring sequences as well as random ones. It is generally the case that over the course of training, performance improves substantially for familiar sequences (sequence-specific learning). Whereas the effect of practice in performing unfamiliar sequences (sequence-nonspecific or general learning) is nonexistent or quite small (Nissen & Bullemer 1987; Keele et al. 2003b; Haider et al. 2018; Verwey et al. 2014; Rhodes et al. 2004; Abrahamse et al. 2013; Moisello et al. 2009; Verwey & Abrahamse 2012; Ghilardi et al. 2009; Deroost & Soetens 2006). While much effort has been put to explaining various mechanisms of sequence-specific learning e.g., associative learning (Perruchet & Pacton 2006) and chunking (Verwey 2001), the general effects of practice remain by and large neglected and poorly understood.

As a main advantage of the proposed design, we were able to reevaluate the computational mechanisms underlying the general learning effects. A dominant view posits that performance in random sequences is purely carried out in *reaction mode* (Verwey & Abrahamse 2012). In line with the Dual Processor Model (Verwey 2001), reaction mode refers to the mode in which a *cognitive processor* maps sequential cues into their appropriate responses one at a time (i.e., action selection). The decided response is then carried out by a *motor processor* (i.e., action execution). This process in referred to as stimulus-to-response

(S-R) mapping. According to this account, any improvements in performing random sequences can thus be attributed solely to a faster and more efficient S-R mapping. Although this seems to be the case for the W=1 condition, our results suggest that there are additional mechanisms at play for W>1.

5.2 Two mechanisms of motor planning/execution: serial and parallel

First, we show that even early on into training, when the effects of learning are minimal, performance significantly benefits form additional cue information with larger window sizes (W, Fig. 3). Specifically, our data demonstrate that sequence execution time (ET) is significantly slower for W=1,2 compared to the full-view condition W=13. This suggests that the motor system utilizes additional information to preplan future actions, and thereby speed up performance by storing multiple prepared actions in the motor buffer in advance (Abrahamse et al. 2013). This immediately opposes the one-by-one loading up of the cues into the cognitive processor in reaction mode (Verwey et al. 2014), at least for W>1. Otherwise, for all window sizes larger than one, we would have expected performance to be equal to the W=1 condition, where performance is strongly governed by one-at-a-time S-R mapping.

Taken together, these results indicate a flexible interplay between motor planning and execution processes, where the dynamics are influenced by the amount of available information about future actions. In W=1 condition, the motor system is assumed to be performing purely in reaction mode, which entails serially planning and then executing the sequentially appearing cues one-by-one. However, in W>1 condition, the motor system is granted the possibility to preplan future presses, as more upcoming cues are available. This entails that in parallel with executing the current press, the preplanning of the future responses to the next-in-line cue(s) is underway.

5.3 Two mechanisms of motor learning: S-R mapping and preplanning

Next, we show that through 5 days of practice, participants demonstrate clear learning effects for all window sizes, as validated by the increasingly faster performance from early to mid and late learning phases (Fig. 4). Furthermore, we found that the effect of practice on

performance is substantially more pronounced for larger window sizes (Fig. 4B). This finding contrasts with, a recent study by Haith et. al. (Haith & Krakauer 2018) promoting a notion which summarizes learning as “caching of the outcome of frequently occurring computations”. This study suggests that practice improves performance through three main avenues: faster S-R mapping, lower cognitive workload and habit formation. These effects of practice are of course hard to question (Lashley 1951; Verwey 2001; Krakauer et al. 2000; Verstynen & Sabes 2011; Wulf et al. 2001; Müller & Sternad 2004). Nevertheless, if these were the only paths through which performance could improve, then for all window sizes larger than one, the magnitude of learning should have turned out equal to the W=1 condition. However, our data points to an additional component of learning which is being overlooked by many accounts.

The next logical question to ask, is the way in which this additional learning mechanism benefits performance. Interestingly, our data demonstrate that the estimated preplanning horizon size keeps monotonically increasing from early to mid and late phases of learning (Fig. 5). This finding, together with the fact that performance benefits more from practice in larger window sizes, make a pivotal suggestion: learning improves performance not only through more efficient S-R mapping (Haith & Krakauer 2018) (W=1), but also through expanding the preplanning horizon size (W>1).

5.3.1 The extent of preplanning modulates current performance

The critical role of preplanning is further emphasized by the fact that throughout sequence execution the eyes are predominantly fixated ahead of the cue being currently executed (Fig. 7 B). This is in line with previous work, showing that gaze location supports planning of future actions during movement (Johansson et al. 2001), as well as reading (Engbert et al. 2002). Additionally, we found that when pressing the first cue in the sequence, eyes fixate furthest away from the press position compared to anywhere else in the sequence. This finding together with the larger initial response time (RT) for larger window sizes (Fig. 6) make the following suggestion: when provided the information, subjects take the time fill the motor buffer (Abrahamse et al. 2013) to its full capacity before initiating movement, i.e., initially preplan as many actions into the future as possible. This in turn posits a possible explanation for the initial inter-press intervals (IPIs) being reliably faster than the middle IPIs

(Fig. 7 A) as follows: having more actions preplanned into the future benefits current performance.

A similar observation has been reported in the literature and attributed to *motor vigor* (Wong et al. 2015), which is thought to enhance by the formation of explicit knowledge about future actions. In the context of the data discussed here, all the sequences are random. However, by that initial time to explore and preplan the first few cues, subjects shape an explicit knowledge of their initial course of action, and hence, perform substantially better at the beginning of every sequence. After this initial phase however, additional cues are revealed one at a time, concurrently with the press progression into the sequence, and thus performance seems to reach a slower steady-state (Fig. 7 A).

5.4 Sequential race model: a candidate mechanism to explain sequence-nonspecific learning

As previously discussed, our data suggest that depending on the availability of in-advance information, the motor system has the ability to operate in two distinct modes: serial and parallel planning/execution. In the former case, cues are translated to responses one-by-one, and subsequently the appropriate motor command in triggered (W=1). Whereas in the latter case, both the planning and execution processes progress in parallel.

We set out to implement this analogy in the context of a sequential race model, to examine its plausibility in replicating the data. We propose a relatively simple cascade-like structure where the response to every single cue in the sequence is represented by an independent accumulator race model between 5 alternative options (Fig. 8).

Race models have been effectively employed to capture diverse processes underlying behavioral, perceptual and oculomotor decision-making (Carpenter & McDonald 2007; Gold & Shadlen 2001; Ratcliff & Rouder 1998). Drift diffusion models with two opposing bounds are readily applied to two-choice tasks (Gold & Shadlen 2001). Our task however, included five response options (fingers thumb to pinky). Thus, similar to the LATER model (Carpenter & McDonald 2007), we consider diffusion to a single upper bound i.e. the response threshold, for each option in the race. Furthermore, our model assumes independence not only between the sequential races within every trial (i.e., presses within a

sequence), but also between the five competitor decision-units within each race (i.e., alternative options). This structure offers a possible candidate mechanism by which sequential actions with multiple alternative responses can be selected on the basis of cued stimuli.

The model was characterized by a fixed delay between stimulus and race onset (visual delay) as well as a second fixed delay between the triggering of the motor command and registration of the press (motor delay). The model was fitted to capture the data by optimizing the following parameters: magnitude of the decision boundary, the evidence accumulation rate which determines the speed with which the cued option in the race approaches the boundary, and finally the preplanning weights ($\lambda_{2-5},\ Eq.6$). Optimization was carried out for early and late learning phases separately.

The insights gained from the model are two-fold: *a)* the implementation of both serial and parallel motor planning/execution is attainable within a unified framework (Fig. 9), which can be optimized to fit the data (Fig. 11 B, C and D). Thereby, we suggest that parallel planning/execution is possible through allocating monotonically decreasing preplanning weights to the next cues, the further away they are into the future. This requires the maximum preplanning weight of 1 to be assigned to the immediately upcoming press ($\lambda_1 = 1$, Fig. 10). In this sense, serial planning/execution would simply mean setting all but the first preplanning weight to zero ($\lambda_{2-14} = 0$).

b) in the context of such a model, learning under the S-R mapping mechanism (W=1), can be attributed to changes in magnitude of the decision boundary, as well as the evidence accumulation rate, as these are the only contributing parameters to replicate the W=1 condition. Whereas, learning by the expansion of the preplanning horizon size can be explained by an increase in the preplanning weights (Fig. 11 A) for the future cues.

Taken together, the model mathematically captures the conceptual properties of parallel and serial planning/execution and offers mechanistic insights into learning effects. However, it is completely naïve to the biomechanical properties of hand function, accounting for which would be the next step towards a more realistic model.

5.5 General conclusions

We designed a novel finger sequence task which allowed us to investigate the poorly understood general effects of practice when performing unfamiliar sequences. We gained new insight into the different modes of motor performance, which are effectively utilized depending on the amount of information provided to the motor system. Furthermore, we provide firm evidence that besides more efficient stimulus-to-response mapping, additional mechanisms contribute to optimizing performance through practice. We suggest that this additional learning mechanism benefits performance through expanding the span of preplanning horizon, as a result of which more future actions can be prepared and stored in the motor buffer in parallel. Finally, we propose a potential computational framework, through which our findings can be partially replicated and explained. This study provides the stepping stone to build more potent experimental designs, enabling a more wholesome view into the mechanisms through which practice benefits behavior. This will in turn, provide solid grounds to computationally model and explain different aspects of motor learning.

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Appendix

Appendix 1: Ethic protocol

Western Research

Date: 20 April 2018

To: Prof. Joern Diedrichsen

Project ID: 108479

Study Title: Studies of the acquisition and control of skilled finger movements.

Application Type: Continuing Ethics Review (CER) Form

Review Type: Delegated

Meeting Date: May 4, 2018

Date Approval Issued: 20/Apr/2018

REB Approval Expiry Date: 15/May/2019

Dear Prof. Joern Diedrichsen,

The Western University Research Ethics Board has reviewed the application. This study, including all currently approved documents, has been re-approved until the expiry date noted above.

REB members involved in the research project do not participate in the review, discussion or decision.

The Western University NMREB operates in compliance with the Tri-Council Policy Statement Ethical Conduct for Research Involving Humans (TCPS2), the Ontario Personal Health Information Protection Act (PHIPA, 2004), and the applicable laws and regulations of Ontario. Members of the NMREB who are named as Investigators in research studies do not participate in discussions related to, nor vote on such studies when they are presented to the REB. The NMREB is registered with the U.S. Department of Health & Human Services under the IRB registration number IRB 00000941.

Please do not hesitate to contact us if you have any questions.

Sincerely,

Daniel Wyzynski, Research Ethics Coordinator, on behalf of Prof. Randal Graham, NMREB Chair

Note: This correspondence includes an electronic signature (validation and approval via an online system that is compliant with all regulations).

Curriculum Vitae

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September 6th, 1986

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Graduate Student, Graduate Program in Neuroscience, Western University

EDUCATION

M.Sc. Neuroscience – WsternUniversity, London, Ontario. 2016-2018

Ph.D. Biomedical Engineering – Tarbiat Modares University, Tehran, Iran. 2012 (discontinued after 3rd year)

M.Sc. Biomedical Engineering – Azad University, Mashhad, Iran. 2010-2012

B.Sc. Electrical Engineering – Azad University, Mashhad, Iran. 2004-2009

TEACHING EXPERIENCE DURING TIME AT WESTERN UNIVERSITY

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ABSTRACTS DURING TIME AT WESTERN UNIVERSITY

Kodjazi, N., Diedrichsen, J., Learning Expand the Planning Horizon in Finger Sequence Tasks, presented at the Neural Control of Movement Meeting, 2018